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NEW FINDS OF A SMALL ANTHROPOID PRIMATE FROM NACHOLA, NORTHERN KENYA

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ABSTRACT Twenty two specimens of a small anthropoid primates, discovered at Nachola during the field seasons of 1982–86, are described in detail. One mandibular fragment is included in the material, but other specimens are isolated teeth, including upper and lower molars and lower premolars. The material is considered to belong to *Nyanzapithecus*.

Key Words : Nachola; Miocene catarrhines; *Nyanzapithecus*; Oreopithecids; East Africa.

INTRODUCTION

For more than half a century, East Africa has been yielding an abundance of Miocene primate fossils, most of these have come from Kenya with some additional specimens from Uganda. These localities of these fossils are distributed mainly in the vicinity of Lake Victoria, western Kenya (Pilbeam, 1969; Andrews, 1978; Harrison, 1982; 1988), although three new species of anthropoid primates were reported in 1980s, from Kalodirr, northern Kenya (Leakey & Leakey, 1986a; 1986b; 1987; Leakey et al., 1988a; 1988b).

The Joint Japan-Kenya Expeditions directed by Dr. H. Ishida has been conducting an ongoing research project on palaeontology and geology in northern Kenya, with a special interest in the evolution of Hominoidea (Fig. 1). Field surveys and excavations in the Nachola area have provided a number of fossils, including a few hundred specimens of Miocene primates. The age of the fossiliferous deposits in Nachola was first estimated as ca. 11–12 Ma by K-Ar dating (Matsuda et al., 1984; 1986), but it may be rather older, based on further studies which give estimations of 13–15 Ma by K-Ar dating, and of 16–17 Ma by faunal analysis (H. Ishida, pers. comm.). Although it is a rare element in the primate material from Nachola, a small oreopithecoid is recognized, and is assigned to *Nyanzapithecus*.

The known material of *Nyanzapithecus* from Kenya is represented only by isolated teeth and several jaw fragments, but the dental features suggest a close relationship with *Oreopithecus bambolii* from the late Miocene of Italy. *Nyanzapithecus* may thus be ancestral to this unique Eurasian primate (Harrison, 1986a). Although *Oreopithecus* has been assigned variously to hominids, hominoids or cercopithecoids by different researchers (Hürzeler, 1949; 1958; Straus, 1963; Szalay & Delson, 1979; Szalay & Langdon, 1985; Delson, 1985; 1986; Delson & Szalay, 1985; Harrison, 1986b; Sarmiento, 1987), it appears most likely from the present evidence of the postcrania and enamel structures that

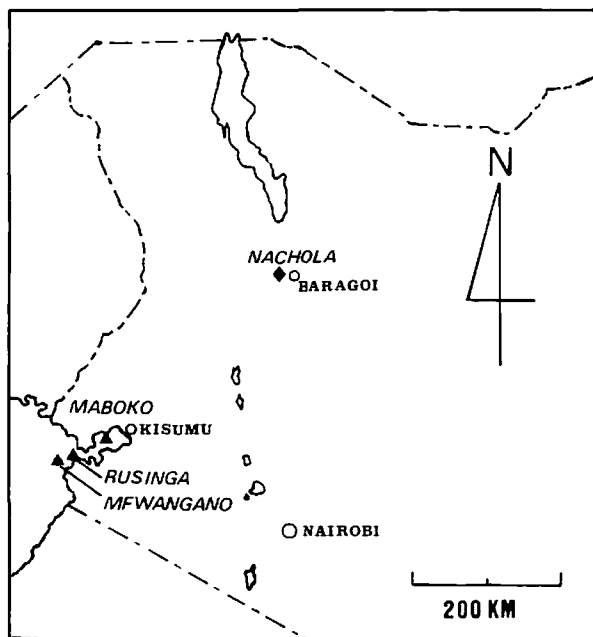


Fig. 1. Map of Kenya, showing the locations of Nachola and other sites of *Nyanzapithecus*.

Oreopithecus belongs to the lineage of the extant apes and hominids, comprising a separate family, Oreopithecidae, in Hominoidea (Harrison, 1986b; Sarmiento, 1987; Martin et al., 1988; Boyde & Martin, 1988).

This paper reports detailed descriptions of the specimens belonging to *Nyanzapithecus* from Nachola.

SYSTEMATICS

Order: Primates Linnaeus, 1758

Suborder: Anthroipoidea Mivart, 1864

Infraorder: Catarrhini Geoffroy, 1812

Superfamily: Hominoidea Gray, 1825

Family: Oreopithecidae Schwalbe, 1915

Genus: *Nyanzapithecus* Harrison, 1986

Generic Diagnosis: Small to medium-sized anthropoid primates ranging in dental size from *Hylobates hoolock* to *Symphalangus syndactylus*. Relatively short face with low, broad nasal aperture and robust premaxilla. Cheek teeth with thick enamel. Upper I1 broad and spatulate, and relatively low-crowned and stoutly constructed with elevated lingual cingulum and weak lingual pillar. Upper I2 broad and low-crowned and robust with well-developed, elevated lingual cingulum. Lower incisors broad and moderately high-crowned. Upper P3 approximating in morphology to P4. Upper premolars long and narrow with a distinct lingual cingulum, at least, on P4. The cusps are inflated and elevated, and of similar

height on P4, but the lingual cusp is slightly lower than the buccal cusp on P3. Lower P3 long and bilaterally compressed with a short mesial ridge, elevated lingual cingulum, and enamel only slightly extended onto the mesiobuccal aspect of the mesial root. Lower P4 longer than broad with high cusps, and the mesial fovea much more elevated than the distal basin. Upper molars, at least M1 and M2, are long and narrow. The cusps are low, rounded and voluminous. The trigon basin and mesial and distal foveae are restricted. The lingual cingulum is well-developed. The occlusal crests are short and rounded. $M1 < M2 = M3$. Lower molars long and narrow with low, rounded and inflated cusps, deeply excavated talonid basin, restricted mesial and distal foveae, reduced buccal cingulum. $M1 < M2 < M3$. Upper dP4 longer than broad with low, rounded and relatively inflated cusps, less restricted basin and foveae relative to the permanent molars (emended from Harrison, 1986a).

Nyanzapithecus sp.

Locality: Nachola, Samburu District, Kenya.

Material: The material consists of a small mandibular fragment with right P3, and twenty two isolated teeth, which represent upper and lower molars and lower premolars (Table 1).

Table 1. List of the specimens and dental measurements of *Nyanzapithecus* sp. from Nachola.

Accession No.		MD*	BL*	Buc.H.	Slope L.
Upper					
BG15236	M1	6.3	6.0		
BG17850	M1	6.2	5.8		
BG15064	M2	6.6	6.8		
BG15232	M2	7.2	7.2		
BG15237	M2	6.8	7.0		
BG15238	M2	7.1	7.2		
BG15344	M3	6.5	7.7		
BG17863	M3	6.6	7.3		
Lower					
BG14709	P3	7.0	4.6	5.3	6.5
BG15329	P3	7.0	4.5	5.0	6.1
BG17844	P3	6.9	4.2	6.2	6.7
BG15318	P4	5.8	4.1		
BG15231	M1	6.2	4.9		
BG15209	M2	7.2	5.8		
BG15228	M2	7.3	5.8		
BG15235	M2	7.8	6.2		
BG15239	M2	7.2	5.7		
BG15240	M2	7.4	5.8		
BG15227	M3	8.5	6.4		
BG15229	M3	7.9	6.3		
BG15230	M3	7.8	6.2		
BG15233	M3	7.7	6.3		
BG15341	M3	8.3	6.8		

* Maximum length and perpendicular breadth for lower P3.

DESCRIPTIONS

I. Mandible (Fig. 2)

BG14709 is a symphyseal fragment with right lower P3 and the roots of right P4, right I1-C & left I1-C. On the buccal surface, the inferior half of the symphysis is depressed, probably due to the postmortem deformation. There is a wide crack on the buccal surface below the right canine, so that the canine root is visible. Just distal to the crack and at about a third of the height of the mandible superior to the inferior margin of the body is a very small and oval depression, which is probably the mental foramen. Although the inferior margin of the symphysis is slightly broken, the inferior transverse torus appears absent or, if developed, very weak. The superior transverse torus is developed at about two thirds of the mandibular height inferior to the alveolar margin, extending backward up to the level of P3. The symphyseal height and thickness are 19.6 mm and 6.0 mm, respectively. The body height and thickness at P4 are 15.9 mm and 5.9 mm, respectively. This specimen is much more gracile relative to the single mandibular specimen (RU1855) attributed to *N. vancoveringi* by Harrison (1986a).

II. Upper Molar (Fig. 3)

BG15236 is a weathered left upper M1 crown. The cusps are slightly worn, and seem to be less inflated than on the second molars, but this might be due to the extensive weathering of the crown. Whether the hypocone is connected to the protocone is not certain due to heavy weathering, but if connected, the connecting ridge must have been quite indistinct.

BG17850 is a left upper M1 with its enamel completely lost. Although the buccal margin is damaged, it seems certain that the crown is slightly longer than broad.

BG15064 is a moderately worn and weathered left upper M2 crown. Small areas of dentine exposure are seen on the protocone and hypocone. The lingual cingulum is well-developed on the mesial aspect of the protocone, but is reduced lingually, becoming almost absent before it reaches the hypocone.

BG15232 is a right upper M2 crown. It is only slightly worn. The lingual surface of the protocone is damaged. A fine groove runs between the hypocone and protocone. A distinct small tubercle is developed in the distal basin, adjoining to the hypocone. There is a very weak ledge mesiobuccal to the paracone.

BG15237 is a slightly worn right upper M2 crown. The lingual cingulum is well-developed mesial to the protocone, but is reduced lingually. A relatively large tubercle is present on the cingulum at the mesiolingual corner of the crown. The crown is waisted with the distal moiety narrower than the mesial moiety.

BG15238 is a moderately worn left upper M2 with small part of the roots. Small chips of enamel are lost from the paracone. Small areas of dentine exposure are seen on the cusps except for the paracone. The main part of the lingual cingulum ends at the mesiobuccal aspect of the hypocone, but a very weak remnant of the cingulum extends onto the lingual aspect of the hypocone.

BG17863 is a slightly worn right upper M3 with a small portion of the roots.

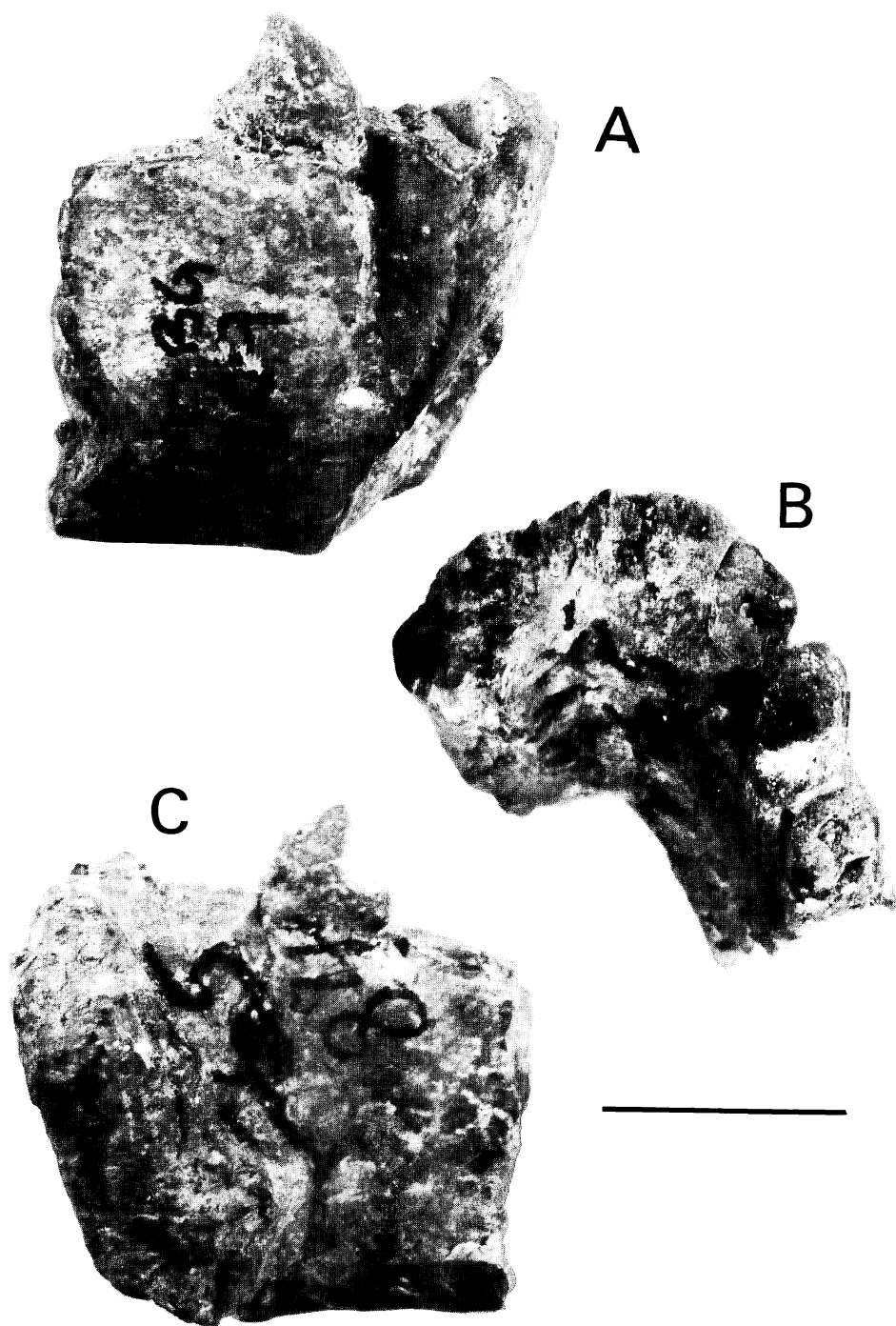


Fig. 2. Mandibular fragment (BG14709) of *Nyanzapithecus* sp. from Nachola; A: buccal aspect, B: occlusal aspect, C: lingual aspect. Scale is 1 cm.

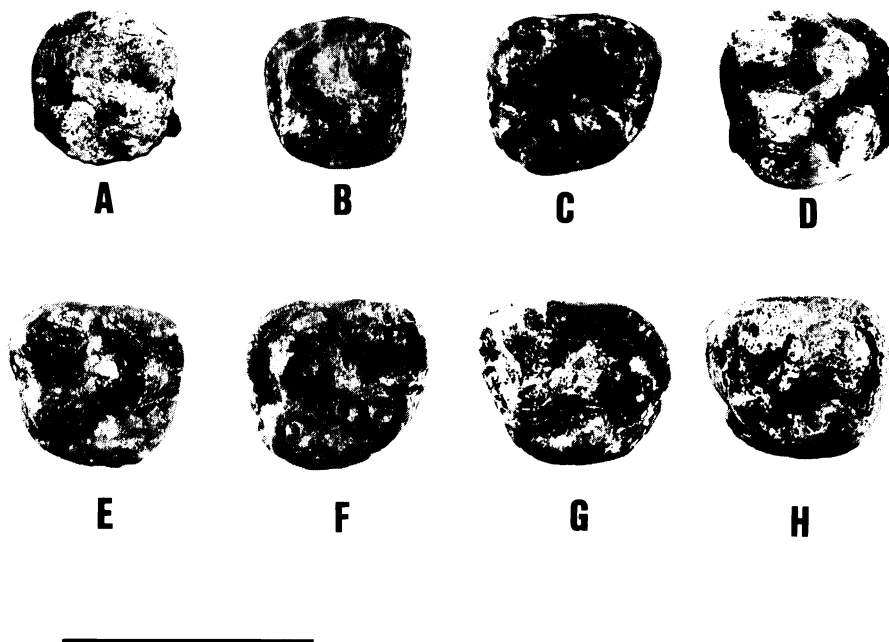


Fig. 3. Occlusal view of the upper molars of *Nyanzapithecus* sp. from Nachola: A; BG15236 (lt M¹), B; BG17850 (lt M¹), C; BG15064 (lt M²), D; BG15232 (rt M²), E; BG15237 (rt M²), F; BG15238 (lt M²), G; BG15344 (rt M³), H; BG17863 (rt M³). Scale is 1 cm.

The metacone is much reduced, and is the smallest cusp. The distal moiety is much narrower than the mesial moiety, giving an occlusal outline of the crown a rounded triangular shape. The lingual cingulum is well-developed both mesially and lingually. However, the cingulum is slightly wider mesially than lingually. Buccally, the paracone is surrounded by a weak cingulum.

BG15344 is a slightly worn right upper M3 crown. The protocone and buccal cusps are only slightly worn, but flat and medium-sized wear facets are seen on the hypocone and on the protoconule region. The hypocone is fused with a well-developed subsidiary tubercle that occupies most of the distal basin. The metacone is much reduced. The lingual cingulum is well-developed mesially, but is reduced lingually, becoming nearly absent before it reaches the hypocone. A small tubercle is weakly developed on the lingual cingulum at the mesiolingual corner of the crown. The buccal cingulum is slightly developed midway up the buccal aspect between the buccal cusps.

III. Lower P3 (Fig. 4)

BG14709 is a right lower P3 rooted in the mandibular fragment. It is low-crowned and bilaterally compressed. The mesial and lingual ridges are low and rounded.

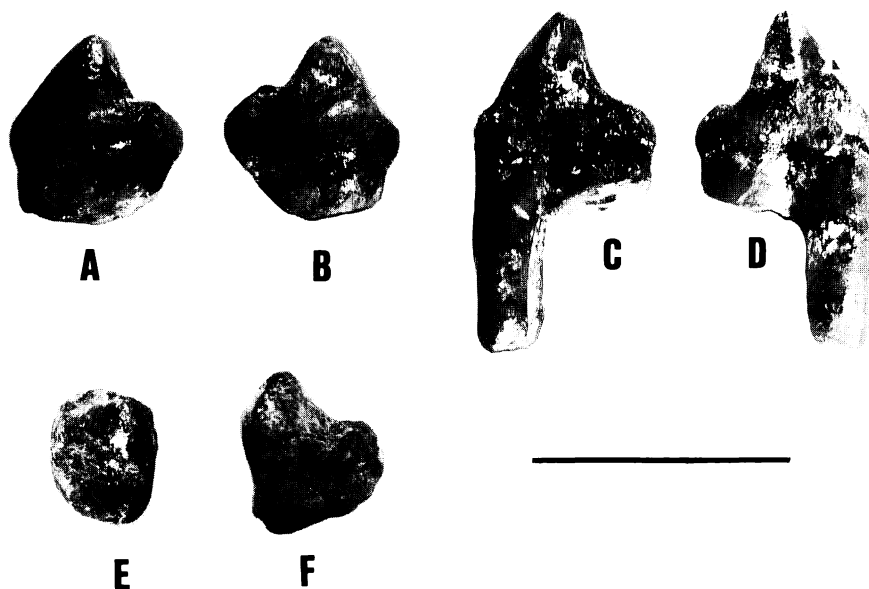


Fig. 4. Lower premolars of *Nyanzapithecus* sp. from Nachola: A & B; buccal and lingual aspects of BG15329 (lt P₃), C & D; buccal and lingual aspects of BG17844 (lt P₃), E & F; occlusal and buccal aspects of BG15318 (lt P₄). Scale is 1 cm.

The distal ridge is poorly defined. The mesial ridge is short, running down to meet with the well-developed and elevated lingual cingulum. The axis of the maximum length is set obliquely relative to the cheek tooth row.

BG17844 is an unworn left lower P3 with the mesial root complete. The crown is high and strongly bilaterally compressed. The three ridges are inflated but pronounced. The mesial ridge is slightly longer than in the other two lower P3 in this material, and joins the well-developed lingual cingulum at a small tubercle. The junction of the lingual ridge with the lingual cingulum also forms a small tubercle. There is a deeply excavated valley between the lingual and distal ridges. The distal basin is strongly concave. The buccal surface is surrounded basally by a continuous and relatively distinct cingulum. The mesiobuccal slope is relatively steep.

BG15325 is an only slightly worn left lower P3 with a small part of the roots. The crown is low and moderately bilaterally compressed. The mesial and lingual ridges are low, rounded and short. The distal ridge is very poorly defined with a small tubercle at the junction with the distal marginal ridge. The short mesial ridge meets with the well-developed lingual cingulum, which forms a narrow ledge between the mesial and lingual ridges. The lingual cingulum ascends mesially. The distal basin is shallow. The lingual surface between the mesial and lingual ridges is flat.

IV. Lower P4 (Fig. 4)

There is only one lower P4 in the material. BG15318 is a weathered and slightly

worn left lower P4 crown. The occlusal outline is ovoid. The crown is long and narrow with the breadth-length index of 70.7 %. The cusps are elevated and closely approximated to each other. The occlusal ridges are low and rounded and poorly defined. The mesial fovea is restricted and much more elevated relative to the distal fovea. There is a short but distinct cingulum mesial to the buccal cusp. There is a low and rounded longitudinal ridge running down from the apex of the buccal cusp to meet with the distal marginal ridge, which extends beyond the junction, down onto the buccal surface. Between the extension of the distal marginal ridge and the distal ridge of the buccal cusp is a shallow depression, which may represent a remnant of the buccal cingulum.

V. Lower Molars (Fig. 5)

BG15231 is a slightly worn left lower M1 crown. The mesial moiety is slightly narrower than the distal moiety. The distal fovea is a shallow pit, being connected to the talonid basin by a groove between the cusps. The buccal cingulum is much reduced to a weak trace mesial to the protoconid, and narrow but distinct pits between the buccal cusps.

BG15209 is a heavily worn left lower M2 with small portion of the roots. The dentine is exposed on all the cusps, but the areas of the exposure are small. Only the areas of dentine exposure on the hypoconid and hypoconulid are linked to each other. These two cusps have suffered most heavily from the occlusal wear. The buccal cingulum is reduced to a weak trace mesial to the protoconid, a pit between the protoconid and hypoconid and a narrow ledge surrounding the distobuccal aspect of the hypoconid.

BG15228 is a moderately worn left lower M2 with 1/3 to 1/2 of the roots. Small areas of dentine exposure are present on all the cusps. The entoconid and hypoconid appear to be linked by a very fine ridge, though occlusal wear made this feature uncertain. The distal fovea is occupied by a moderately well-developed subsidiary tubercle. The buccal cingulum is moderately reduced. It is divided into three narrow but distinct ledges which are developed mesial to the protoconid and between the buccal cusps. The latter two ledges appears to be linked by a weak trace.

BG15235 is an only slightly worn left lower M2 crown. The entoconid is linked to the hypoconid by a low and fine ridge. The small distal fovea is occupied by a well-developed subsidiary tubercle. The buccal cingulum is much reduced.

BG15239 is a heavily worn right lower M2 crown. The dentine is exposed on all the cusps, but the areas of dentine exposure are small. The hypoconid and hypoconulid are the most heavily worn cusps. The buccal cingulum is reduced to a short ledge between the protoconid and hypoconid.

BG15240 is a moderately worn right lower M2 crown. The mesial fovea is narrow and quite long because of the distally displaced mesial transverse ridge. The distal fovea is completely occupied by a well-developed subsidiary tubercle. The buccal cingulum is moderately reduced to a weak trace mesial to the protoconid, and a narrow ledge which begins at the distobuccal surface of the protoconid and ends at the mesiobuccal surface of the hypoconulid. The hypoconulid is separated

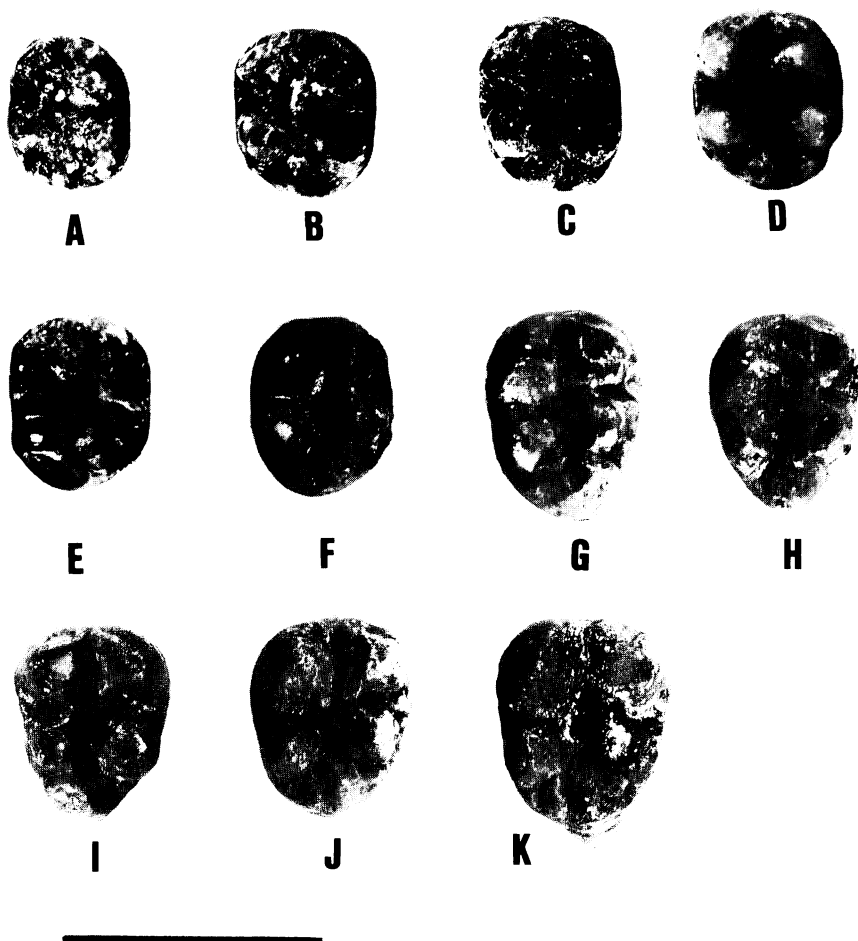


Fig. 5. Occlusal view of the lower molars of *Nyanzapithecus* sp. from Nachola: A; BG15231 (lt M₁), B; BG15209 (lt M₂), C; BG15228 (lt M₂), D; BG15235 (lt M₂), E; BG15239 (rt M₂), F; BG15240 (rt M₂), G; BG15227 (rt M₃), H; BG15229 (rt M₃), I; BG15230 (lt M₃), J; BG15233 (rt M₃), K; BG15341 (rt M₃). Scale is 1 cm.

from the entoconid by a distinct groove.

BG15227 is a moderately worn right lower M3 crown. The dentine is exposed on all the buccal cusps, but is not exposed on the lingual cusps. The crown tapers distally, forming the triangular occlusal outline. The hypoconulid is large, and is displaced medially so as to be close to the entoconid, and almost obliterating the distal fovea. There is a moderately distinct ledge mesial to the protoconid. A continuous ledge, beaded with four well-developed small tubercles, surrounds the buccal aspect of the crown from the distobuccal aspect of the protoconid to the buccal side of the hypoconulid.

BG15229 is a heavily worn right lower M3 crown. A medium-sized area of dentine exposure is present on the protoconid, but there are only very small areas of dentine exposure on the other four cusps. The hypoconulid is slightly medially displaced. The buccal cingulum is reduced to a short ledge mesial to the protoconid, a distinct ledge between the protoconid and hypoconid, and a weak trace surrounding the distobuccal surface of the hypoconid.

BG15230 is a moderately worn left lower M3 with small part of the roots. A chip of enamel is lost from the hypoconulid. Small areas of dentine are exposed on the protoconid, hypoconid and metaconid. The hypoconulid is slightly medially displaced, reducing the distal fovea to a small pit. The hypoconulid and entoconid are separated by a distinct groove. The buccal cingulum is moderately reduced and discontinuous. Whether there is any connection between the entoconid and hypoconid is not certain due to the occlusal wear, but it appears possible that a fine ridge linked the two cusps before wearing.

BG15233 is an only slightly worn right lower M3 with a small portion of the mesial root. There is a very small tubercle between the metaconid and hypoconid. The distal fovea is almost obliterated because of the development of a small tubercle on the distolingual side of the hypoconulid. The buccal cingulum is moderately developed, and is continuous along the buccal length of the crown, being decollated by some bead-like small tubercles.

BG15341 is a heavily worn right lower M3 with 1/3 of the roots. The buccal surface of the protoconid is damaged. The entoconid is reduced. There is a small tubercle in the talonid basin between the entoconid and hypoconid. The distal basin is occupied by a small tubercle developed lingual to the hypoconulid. The buccal cingulum is relatively well-developed.

DISCUSSION

There are two previously recognised species in *Nyanzapithecus*. *N. pickfordi* is relatively well represented, but another species, *N. vancouveringi*, is only poorly known. They were reported from Rusinga, Mfangano and Maboko, all of which are small islands in Lake Victoria, western Kenya (Harrison, 1986a; Kunitatsu, 1992).

The new material described in this paper is the first find of *Nyanzapithecus* from northern Kenya, whose locality is situated some 350 km north to Nairobi.

The upper and lower molars from Nachola are relatively shorter than in *N. pickfordi* or *N. vancouveringi*, although they show a tendency of crown elongation relative to the early Miocene proconsulids. The breadth-length index of upper M1 is slightly higher in the material than in *N. vancouveringi*, but the measurements of both specimens from Nachola are estimated values due to the damage on the crowns. Also, the upper third molars show a strong reduction of the distal moiety, especially on the metacone. Hence the crown is broader than long with the average for the breadth-length index of 87.4 %. In addition, the lower third molars are also relatively shorter, and are similar in proportion to those of the early Miocene proconsulids. The elongated molars probably indicate a folivorous diet. Among

the extant hominoids, *Symphalangus syndactylus* (Siamang), considered to be more folivorous than *Hylobates*, have the longest molars. Although the molars of the great apes are rather shorter than those of hylobatids, *Gorilla*, more folivorous than the other great apes, has generally the longest molars among them. Probably, the species from Nachola had already taken a step toward an adaptation for folivorous diet, but not to the extent seen in *Nyanzapithecus* from western Kenya.

An interesting dental feature of the material from Nachola is the presence of a weak but continuous cingulum surrounding the base of the buccal surface of the lower third premolars. It is present on all the three lower P3 in the material. Such a cingulum is not seen in the other Miocene non-cercopithecoid catarrhines from East Africa, including the single specimen of lower P3 belonging to *N. pickfordi*. It should be noted that a similar cingulum is developed in *Oreopithecus bambolii* (Hürzeler, 1949; 1958).

Another dental feature to be mentioned, though its phylogenetic or functional meaning is not certain, is a well-developed tubercle on the lingual cingulum at the mesiolingual corner of the upper M2 (BG15237). Among the other Miocene non-cercopithecoid catarrhines, the type of *Turkanapithecus kalakolensis* has a tubercle at the same position on the upper M2, though the molar is quite heavily worn (Leakey et al., 1988b). One upper M2 (SO375) of *Rangwapithecus gordonii* also shows an extensive swelling on the lingual cingulum, but it is not a common feature for the species. In modern humans, the cusp of Carabelli is a well-known variation of the upper molars. It is a subsidiary tubercle sometimes developed on the mesiolingual aspect of the protocone in various shape and size. When he mentioned to the cusp of Carabelli in his short review on human dentition, Setoguchi (1986) called attention to the presence of the pericone, which is a unique cusp developed on the mesiolingual aspect of the protocone in an Eocene primate, *Periconodon*. Although we cannot say much about the homology of these tubercles, the appearance of a similar tubercle at the same position should be noted.

In addition to this subsidiary tubercle on the upper molar, the lower molars from Nachola also have a tendency to develop a subsidiary tubercle in the distal fovea, which may correspond to the sixth cusp in modern humans. This tubercle is seen, at least, on three second molars ($3/5 = 60\%$) and two third molars ($2/5 = 40\%$). Also, the buccal cingulum is beaded with small tubercles on three lower third molars ($3/5 = 60\%$). In general, the molars of the present material are characterized by a tendency to develop subsidiary tubercles. The considerable development of the subsidiary tubercles, together with the thick molar enamel, may suggest a hard and fibrous diet.

Considering the morphological polarity among oreopithecids, *N. pickfordi* is the most derived species in the genus in such characters as the elongation of the molar crowns, the inflation of the cusps, the restriction of the occlusal basins and foveae, and the particular development of the lingual cingulum on the mesial aspect of the protocone. The material from Nachola appears to be less derived even than *N. vancouveringi* in such a feature as the molar proportion, but might be more derived in the degree of inflation of the molar cusps.

Overall, the morphology of the molars from Nachola suggests that the material is more similar to *N. vancouveringi* from early Miocene than to *N. pickfordi* from

middle Miocene. However, there are some minor differences in size and morphology, so that it is quite probable that the material from Nachola may represent a new species of *Nyanzapithecus*.

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